

Marine nematodes of the family Draconematidae (Nemata): a synthesis with phylogenetic relationships

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Abstract

The family Draconematidae is reviewed. Diagnoses of all taxa are updated or emended, based upon an evaluation of diagnostic features. A phylogenetic analysis at the genus level based on parsimony suggested that *Tenuidraconema* belongs to the Draconematinae. A new genus *Bathychaetosoma* is erected to accommodate *B. uchidai* (Kito, 1983). It is characterized by a cephalic region with a smooth, non-thickened cuticle and numerous cephalic adhesion tubes located posterior to the head region and extending over more than two head diameters along the cervical region.

Introduction

Representatives of the family Draconematidae, when displaying the typical draconematid habitus, are particularly easy to identify at low magnification, even by non specialists. They occur in a large range of habitats, from the pole to the equator and from the intertidal exposed sands to deep-sea hydrothermal vents. They are quite common in algal habitats.

The Draconematidae, together with the Epsilonematidae and Desmodoridae, belong to the superfamily Desmodoroidea Filipjev, 1922. The three families form a monophyletic (= holophyletic sensu Lorenzen) group based on the synapomorphy (= holapomorphy) that only the anterior testis is present (Lorenzen, 1974, 1981, 1994) and established by the synapomorphy that the lip region is clearly separated from the remainder of the cephalic region according to Vincx (1986, p. 269). Currently, only two of the three families i.e. Epsilonematidae and Draconematidae are shown to be monophyletic. The Draconematidae are characterized by three autapomorphic characters: (1) ovaries situated anteriorly to the dorsal bent of the body; (2) adhesive setae in the posterior part of the body, posterior to the ovaries and (3) adhesive setae at the dorsal side of the anterior end. A synthesis of the closely related family

Epsilonematidae was recently published (Gourbault & Decraemer, 1996). This paper is a complement to the study of Desmodoroidea; for data on the Desmodoridae see Vincx (1986).

A first and extensive revision of the draconematids was made by Allen and Noffsinger (1978). They treated the group at superfamily level, Draconematoidea Filipjev, 1918. Two families were distinguished: Draconematidae Filipjev, 1918 and Prochaetosomatidae Allen & Noffsinger, 1978. The family Prochaetosomatinae was created for draconematid species characterized by a non- or slightly swollen pharyngeal region, a pharynx with cylindrical corpus and swollen end bulb, and a buccal cavity usually moderately developed and armed with a dorsal tooth. Allen & Noffsinger (1978) further subdivided the Prochaetosomatidae in four new subfamilies: Prochaetosomatinae, Cygnoneematinae, Dracognomatinae and Notochaetosomatinae. This high taxonomic ranking was not accepted by Lorenzen (1981; 1994 p.155), who downgraded the taxa by one rank and synonymized the last three subfamilies with Prochaetosomatinae, a classification currently followed. Decraemer (1989) attempted a primary phylogenetic analyses of diagnostic characteristics at genus level.

Material and methods

The amount of material collected mostly during tropical field-trips and deep-sea cruises (see acknowledgement), and studied recently (see Decraemer, Gourbault, Verschelde and Vincx in references) constitutes the basis of this study. Some of the types available from different collections have been observed, and other data are from the literature cited. Redescription of species or additional data are recorded between brackets in the species list.

Phylogenetic relationships between 14 Draconematid genera were inferred from a parsimony analysis of 13 taxonomically relevant characters. To this end the 'implicit enumeration (ie*)' option of the program Hennig 86, version 1.5 (Farris, 1989) was applied in combination with the 'Nelsen' command to produce a strict consensus tree.

The polarity of characters was determined on the basis of ontogenetic criteria and the complexity of characters. A hypothetical ancestor with plesiomorphic states for all characters was chosen because no existing taxa could be identified as consistent outgroup. However, the character combination of the outgroup largely agrees with the family Desmodoridae. The plesiomorphic state of each character was coded 0 and the apomorphic states were scored 1 or more. The characters were considered unordered (= non-additive) because the direction of character evolution could not be specified in multistate transformation series. Intra-generic variable characters were dealt with by splitting up one genus in two taxa (see Table 2).

Taxonomy

At present we recognize 14 genera and 70 species of Draconematidae within two subfamilies; the Draconematinae with three genera and 40 species, and the Prochaetosomatinae with eleven genera and 30 species.

Family Draconematidae Filipjev, 1918

Draconematidae: Desmodoroidea. Body short, S-shaped usually with a more or less pronounced, enlarged pharyngeal and mid-body region. Body cuticle annulated except for helmet and tail end often with minute vacuoles (= dotted). Annules usually smooth, rarely with spines or minute vacuoles/granules. Cephalic sensory organs in three circles: 6 anterior labial papillae, 6 short posterior labi-

al setae and 4 cephalic setae. Helmet present (except in *Dinetia*). Amphidial fovea spiral to elongate loop-shaped, rarely reduced with inverted "U"-shape or tubular, located sublateral to dorsolateral on helmet, when present, or near anterior body end. Cephalic adhesion tubes (CAT or cephalic ambulatory setae) present, located dorsally on helmet, just posterior to helmet or in cervical region; absent in the first juvenile stage only. Somatic setae arranged in eight longitudinal rows; four rows in tail region. Buccal cavity narrow to well developed, usually armed with a dorsal tooth, with or without two smaller subventral teeth. Pharynx either dumbbell-shaped or largely cylindrical with or without well defined terminal bulb (with medium swelling in *Dracognomus*). Excretory system absent. Posterior adhesion tubes (PAT or posterior ambulatory setae) arranged in 4 longitudinal rows: 2 sublateral and 2 subventral rows (except *Prochaetosoma vitielloi* with posteriorly a single ventral row) located in the posterior third of the body; PAT with or without differentiated (= bell-shaped) tip, usually straight, rarely long flexible. Female reproductive system anterior to the PAT-region. Males with one testis; copulatory apparatus with two spicules and a trough-shaped gubernaculum. Three caudal glands usually extending beyond the anal region.

Subfamily Draconematinae Filipjev, 1918

Draconematidae. Pharynx dumbbell-shaped (=swollen anterior corpus and posterior bulb), no thickened lumen wall in bulb. Swollen anterior body region usually conspicuous and short. CAT with clearly open tip, mainly blister-shaped, and enlarged base of insertion, located on helmet. Cephalic acanthiform setae may be present on helmet. Buccal cavity narrow, unarmed. Posterior adhesion tubes short and straight (except *Draconema trispinosum* with some longer tubes), with bell-shaped tip. All PAT anterior to cloaca (except in *Dracograllus eira*, *D. minutus*); all PAT anterior to anus except in most *Dracograllus* species. Copulatory thorns rare. Paravulvar seta present or not. Tail cylindro-conoid with numerous annules.

Type genus: Draconema Cobb, 1913.

Remark: Upon the results of the phylogenetic analyses (see further), the pharynx within the Draconematinae comprises one exception: a largely cylindrical pharynx with a terminal bulb.

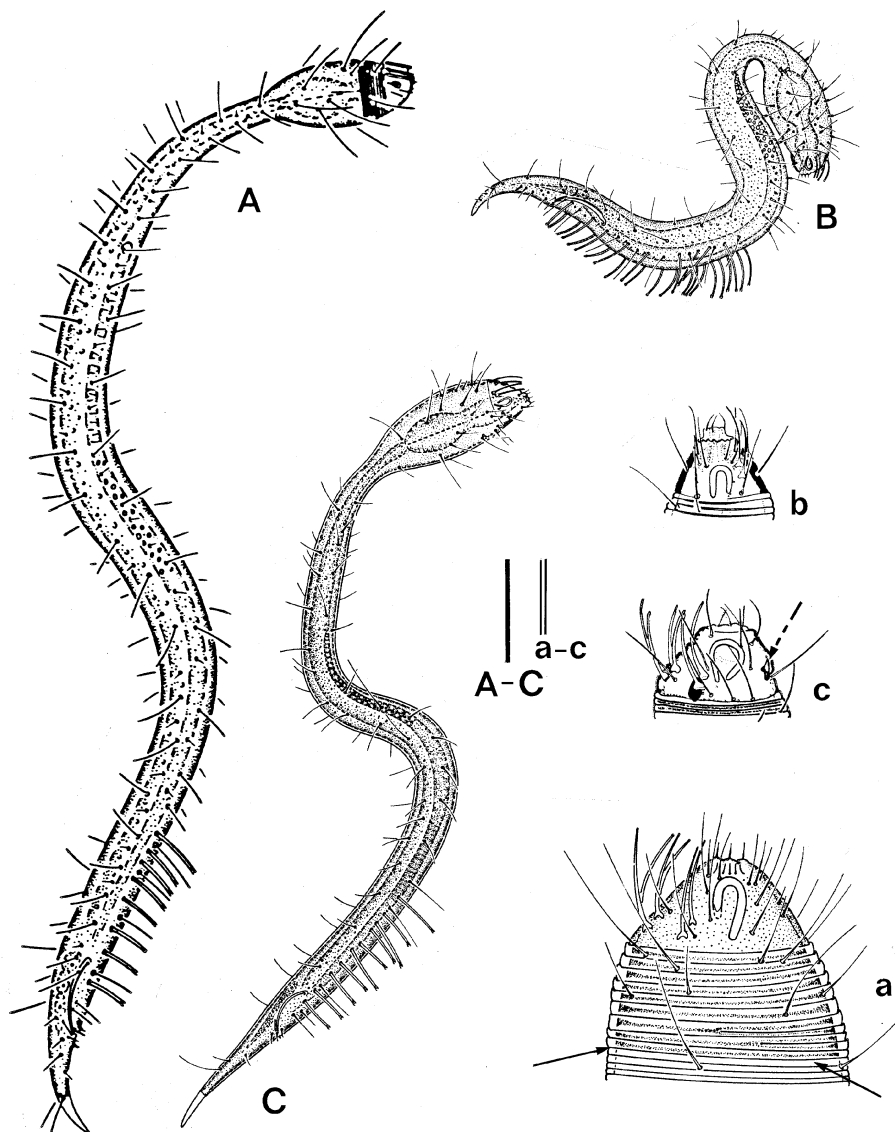


Figure 1. Pictorial key to current genera of the Draconematinae: (A) *Draconema* [*D. cephalatum*]; (a) head of *D. ophicephalum*] arrow at base of the anteriormost annules (7–14) larger with subcuticular granulation; (B) *Dracograllus* [*D. cobbi*]; (b) head of *D. antillensis*]; (C) *Paradraconema* [*P. floridense*]; (c) head] arrow on cephalic acanthiform seta - eyespot, dark spot near head base. Bar = 80 μ m and double bar = 20 μ m. (A, a, B, C: after Allen & Noffsinger, 1978; b: after Decraemer & Gourbault, 1986; c: after Decraemer, 1982).

Genus Draconema Cobb, 1913 (Figure 1A, 1a; 7A–C; 8M)
 syn. *Chaetosoma* Claparède, 1863; *Drepanonema* Cobb, 1933; *Claparediella* Filipjev, 1934; *Tristic-ochaeta* Panceri, 1876

Draconematinae. Swollen anterior body region 10–

13% of total body length. Annulation body cuticle differentiated: anteriormost annules (7–14) larger with subcuticular granulation; cuticle thin. Twelve CAT located on helmet in two transverse rows. Amphids usually with sexual dimorphism in shape: loop-shaped in male, open spiral or unispiral in female, located laterodorsally on helmet. Two pairs of paravulval setae,

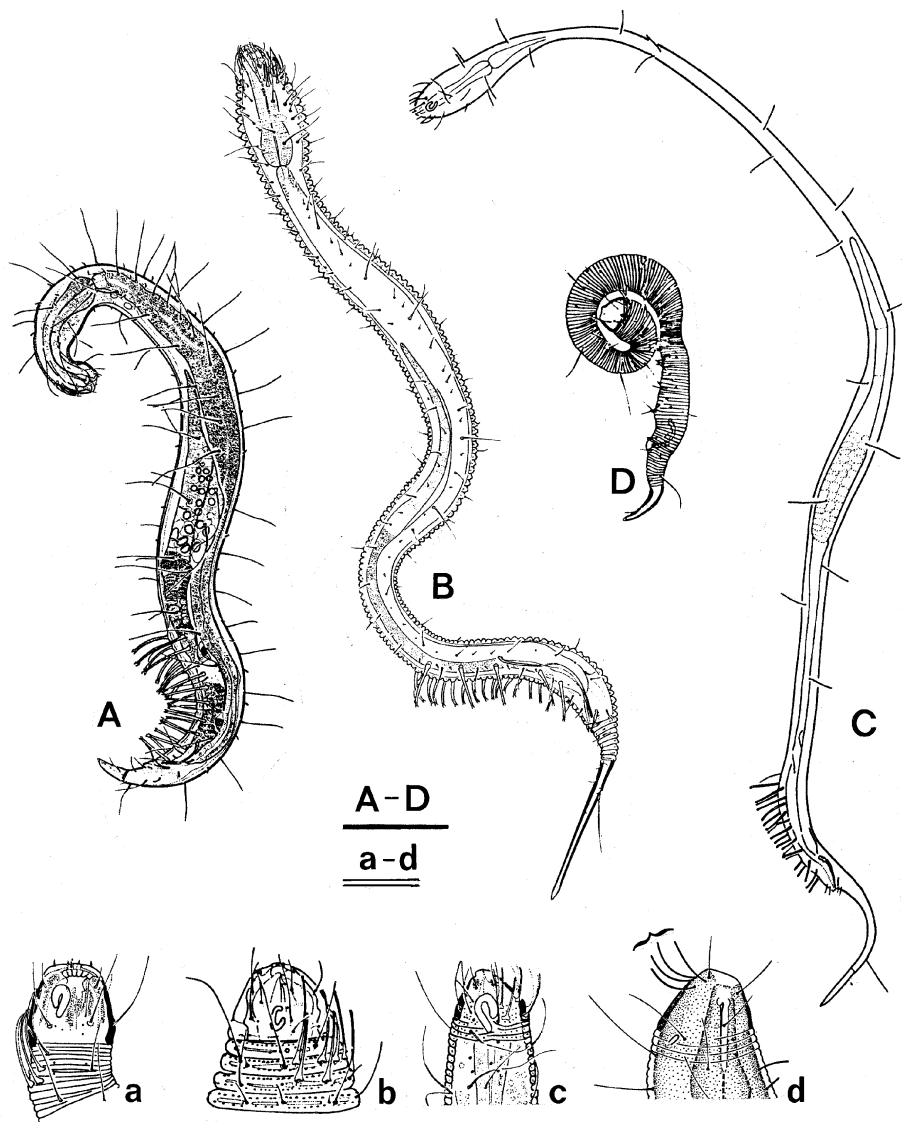


Figure 2. Pictorial key to current genera of the Prochaetosomatinae: (A) *Prochaetosoma* [*P. martensi*; (a) head]; (B) *Apenodraconema* [*A. chlidosis*; (b) head]; (C) *Tenuidraconema** [*T. fiersi*; (c) head] lateral alae not shown; (D) *Dracognomus* [*D. simplex*; (d) head of *D. marioni*, female asymmetrical, ventral side shorter, modified CAT (}) and typical inverted U-shaped amphid clear. Bar = 80 μm and double bar = 20 μm (A, a, C, c: after Decraemer, 1989; B, b: after Gourbault & Decraemer, 1992; D: after Decraemer & Gourbault, 1986; d: after Allen & Noffsinger, 1978). * *Tenuidraconema* belongs to the Draconematinae following present phylogenetic analysis.

one anterior and one posterior to vulva (except in *D. japonicum*). All PAT anterior to cloacal opening/anus.

Type species: Draconema cephalatum Cobb, 1913

– *antarcticum* Allen & Noffsinger, 1978; [Pastor de Ward, 1988]

– *cephalatum* Cobb, 1913; [Allen & Noffsinger, 1978] syn.: *Chaetosoma cephalatum* (Cobb, 1913) Steiner,

1921; *Tristicochaeta cephalatum* (Cobb, 1913) Cobb, 1935

– *chilense* Allen & Noffsinger, 1978

– *claparedii* (Mechnikov, 1867) Filipjev, 1918; [Allen & Noffsinger, 1978; Masallès, 1985]

syn.: *Chaetosoma claparedii* Mechnikov, 1867; *C. armatum* Giard & Barrois, 1874, *C. macrocephalum*

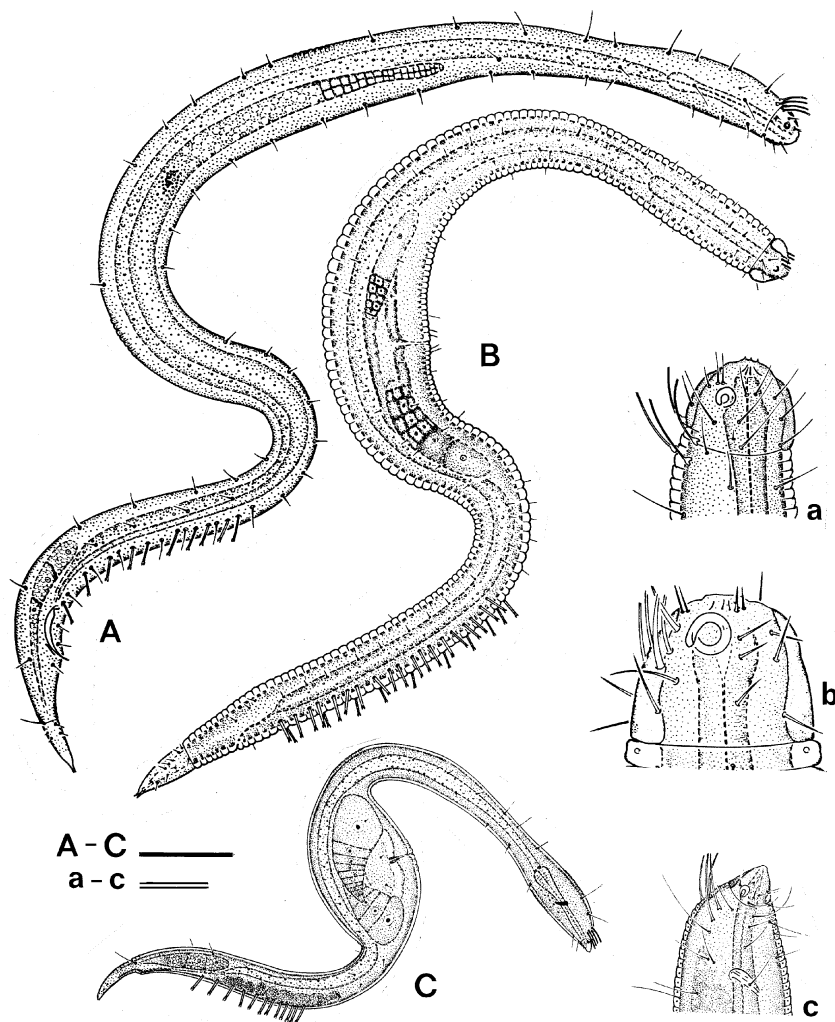


Figure 3. Pictorial key to genera of Prochaetosomatinae: (A) *Notochaetosoma* [*N. tenax*; (a) head]; (B) *Dracogalerus* [*D. afrikaanus* female; (b) head of *D. bastiani* female]; (C) *Draconactus* [*D. cutus* female; (c) head]. Bar = 80 μm and double bar = 20 μm (after Allen & Noffsinger, 1978).

Schepotieff, 1907, *C. hibernicum* Southern, 1914; *Draconema armatum* (Giard & Barrois, 1874) Filipjev, 1918; *D. macrocephalum* (Schepotieff, 1907) Filipjev, 1918; *Notochaetosoma claparedii* (Mechnikov, 1867) Cobb, 1929; *N. armatum* (Giard & Barrois, 1874) Cobb, 1929; *N. macrocephalum* (Schepotieff, 1907) Cobb, 1929; *N. hibernicum* (Southern, 1914) Cobb, 1929; *Drepanonema claparedii* (Mechnikov, 1867) Cobb, 1933; *D. armatum* (Giard & Barrois, 1874) Cobb, 1933; *D. hibernicum* (Southern, 1914) Cobb,

1933; *Claparediella claparedii* (Mechnikov, 1867) Filipjev, 1934; *C. macrocephala* (Schepotieff, 1907) Filipjev, 1934; *Draconema macrocephalum* (Schepotieff, 1908) Schuurmans Stekhoven, 1935; *D. hibernicum* (Southern, 1914) Kreis, 1938 – *haswelli* (Irwin-Smith, 1918); [Allen & Noffsinger, 1978] syn.: *Chaetosoma haswelli* Irwin-Smith, 1918; *Notochaetosoma haswelli* (Irwin-Smith, 1918) Cobb, 1929; *Draconema bandaensis* Kreis, 1938; *Tristic-*

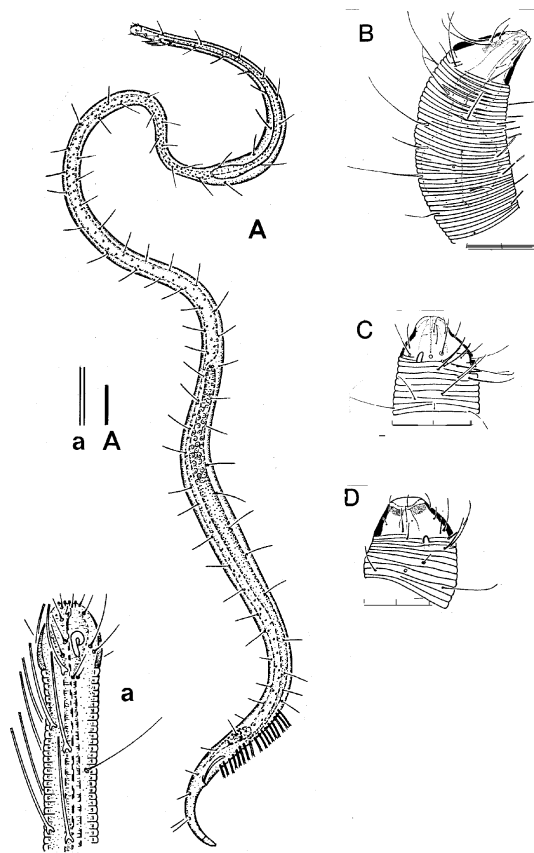


Figure 4. Pictorial key to genera of Prochaetosomatinae: *Cygnone-ma* [*C. steineri*; (a) head]. Bar = 80 μm and double bar = 20 μm (after Allen & Noffsinger, 1978). Shape of amphideal fovea in *Dracognomus*. (B) *D. marioni*, male; (C, D) *D. simplex*, male resp. female; scale 20 μm (B–D: after Decraemer & Goubault, 1986).

ochaeta haswelli (Irwin-Smith, 1918) Johnston, 1938
– *japonicum* Kito, 1976, [1979]
– *ophicephalum* (Claparède, 1863) Filipjev, 1918 [Allen & Noffsinger, 1978]
syn. *Chaetosoma ophicephalum* Claparède, 1863; *C. annulatum* Ditlevsen, 1915; *Draconema cephalatum* Steiner, 1916 nec. Cobb, 1913; *D. cephalatum* Filipjev, 1918 nec. Cobb, 1913; *D. ponticum* Filipjev, 1918; *D. micoletzkyi* Kreiss, 1928; *Notochaetosoma ophicephalum* (Claparède, 1863) Cobb, 1929; *N. annulatum* (Ditlevsen, 1915) Cobb, 1929; *Drepanonema ophicephalum* (Claparède, 1863) Cobb, 1933; *D. annulatum* (Ditlevsen, 1915) Cobb, 1933; *Claparediella ophicephala* (Claparède, 1863) Filipjev, 1934; *C. annu-*

latum (Ditlevsen, 1915) Filipjev, 1934; *Draconema annulatum* (Ditlevsen, 1915) Schuurmans Stekhoven, 1935; *Tristicochaeta ponticum* (Filipjev, 1918) Cobb, 1935; *T. micoletzkyi* (Kreis, 1928) Cobb, 1935.

Genus *Dracograllus* Allen & Noffsinger, 1978

(Figures 1B, 1b; 6A–P; 6'Q–X)

syn. *Dracotoranema* Allen & Noffsinger, 1978

Draconematinae. Swollen anterior body region 18–25% of total body length. Cuticle thin and smooth. Usually eighth CAT on helmet; rarely 10–15. Amphids lateral, usually loop-shaped (equally long branches less common) in both sexes, rarely a derived spiral in female. Precloacal copulatory thorns usually absent. PAT all anterior to cloacal opening (except in *D. eira*, *D. minutus*); PAT usually extending posterior to anus in female (four exceptions). Paravulvar setae may be present.

Type species: *Dracograllus cobbi* Allen & Noffsinger, 1978

– *antillensis* Decraemer & Goubault, 1986
– *chiloensis* Clasing, 1980
– *chitwoodi* Allen & Noffsinger, 1978
– *cobbi* Allen & Noffsinger, 1978
– *cornutus* Decraemer, 1988
– *demani* Allen & Noffsinger, 1978 [Decraemer, 1988; Verschelde & Vincx, 1993]
– *eira* (Inglis, 1968) Allen & Noffsinger, 1978; [Decraemer, 1988; Verschelde & Vincx, 1993]
syn. *Draconema eira* Inglis, 1968
– *falcatus* (Irwin-Smith, 1918) Allen & Noffsinger, 1978

syn. *Chaetosoma falcatum* Irwin-Smith, 1918; *Notochaetosoma falcatum* (Irwin-Smith, 1918) Cobb, 1929; *Drepanonema falcatum* (Irwin-Smith, 1918) Cobb, 1933; *Claparediella falcatum* (Irwin-Smith, 1918) Filipjev, 1934; *Draconema falcatum* (Irwin-Smith, 1918) Kreis, 1938; *Tristicochaeta falcata* (Irwin-Smith, 1918) Johnston, 1938
– *filipjevi* Allen & Noffsinger, 1978
– *gerlachi* Allen & Noffsinger, 1978
– *gilbertae* Verschelde & Vincx, 1993
– *grootaerti* Decraemer, 1988
– *kreisi* Allen & Noffsinger, 1978
– *laingensis* Decraemer, 1988
– *mawsoni* Allen & Noffsinger, 1978
– *minutus* Decraemer, 1988 [Goubault & Decraemer, 1992]

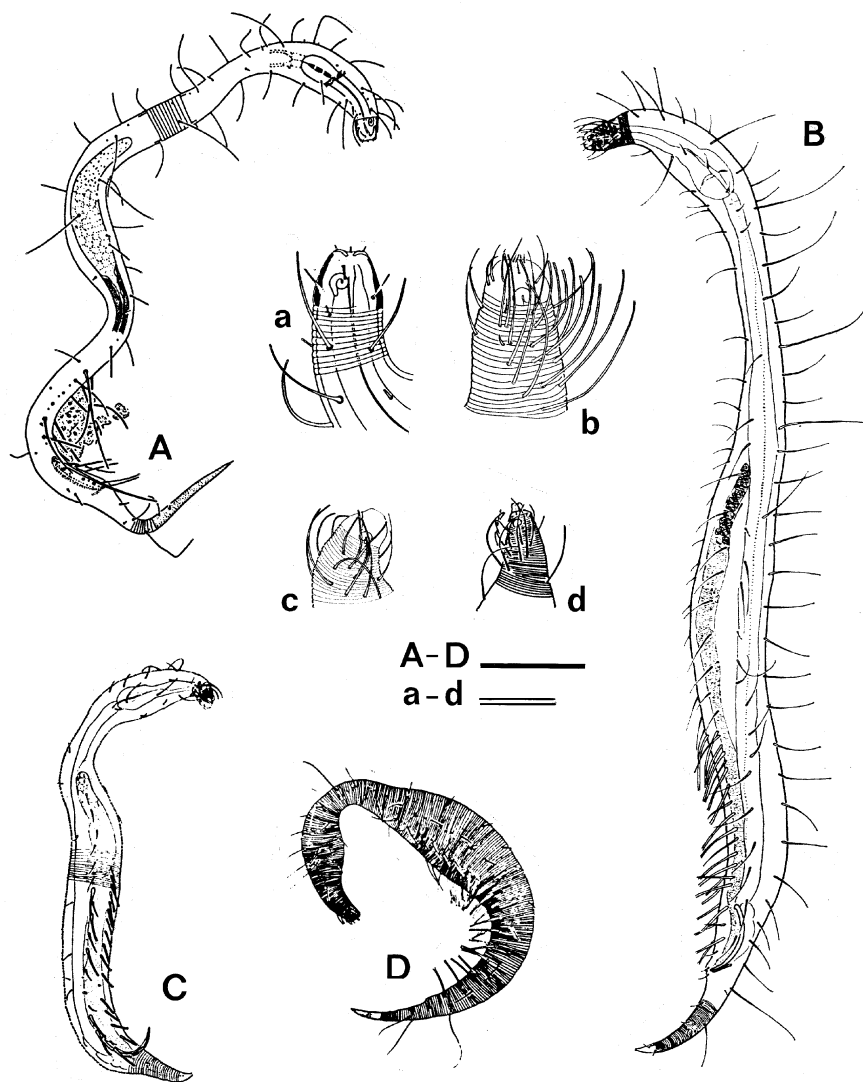


Figure 5. Pictorial key to deep-sea genera of Prochaetosomatinae: (A, a) draconematid gen.n. in Bussau; (B) *Cephalochaetosoma* [*C. pacificum*; (b) head]; (C) *Bathychaetosoma* [*B. uchidai*; (c) head] cephalic region smooth without thickened cuticle; (D) *Dinetia* [*D. nycterobia*; (d) head] body annulation reaching the lipregion, including the spiral amphid. Bar = 80 μ m and double bar = 20 μ m (A, a: after Bussau, 1993; B, b, C, c: after Kito, 1983; D, d: after Decraemer & Gourbault, 1997).

- *papuensis* Decraemer, 1988
- *pusillus* Decraemer, 1988
- *solidus* (Gerlach, 1952) Allen & Noffsinger, 1978
syn. *Draconema solidum* Gerlach, 1952
- *spinosus* Decraemer, 1988
- *stekhoveni* Allen & Noffsinger, 1978
- *timmi* Allen & Noffsinger, 1978 [Gourbault & Decraemer, 1992]
- *trispinosus* (Allen & Noffsinger, 1978) Decraemer,

- 1988
- syn. *Dracotoranema trispinosum* Allen & Noffsinger, 1978
- *wieseri* Allen & Noffsinger, 1978

Remarks

- *D. stekhoveni* shows morphological features characteristic of two genera: (1) *Dracograllus*: swollen anterior body region 19% of total body length, cuticle

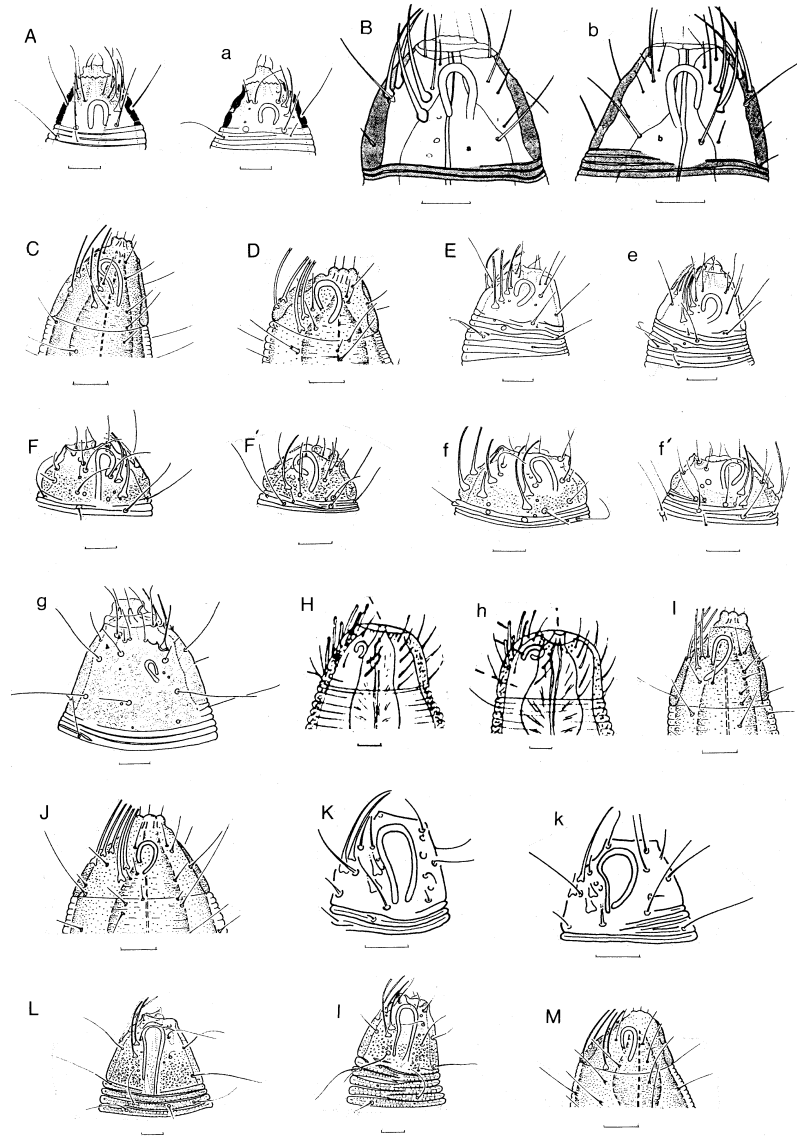


Figure 6a. Different type of amphideal fovea and its variability in male and female of the genus *Dracograllus*: (A, a) *D. antillensis*, male, female; (B, b) *D. chiloensis*, male, female; (C) *D. chitwoodi*, male; (D) *D. cobbi*, male; (E, e) *D. cornutus*, male, female; (F, F', f, f') *D. demani*, males, females; (g) *D. eira*, female; (H, h) *D. falcatus*, male, female; (I) *D. filipjevi*, male; (J) *D. gertlachi*, male; (K, k) *D. gilbertae*, male, female; (L, l) *D. grootaerti*, male, female; (M) *D. kreisi*, male; (N, n) *D. laingensis*, male, female; (O) *D. mawsoni*, male; (P, p) *D. minutus*, male, female. Scale 10 μ m. (A, a: after Decraemer & Gourbault, 1986; B, b: after Clasing, 1980; C, D, I, J, M: after Allen & Noffsinger, 1978; E, e, F, F', f, f', g, L, l: after Decraemer, 1988; H, h: after Irwin-Smith, 1918; K, k: after Verschelde & Vincx, 1993).

smooth, PAT in female posterior to anus and male without preloocal thorns; (2) *Paradraconema*: presence of acantiform cephalic setae, presence of eyespots and a high number of CAT (14–15) arranged on 3 transverse rows.

– Preloocal thorns are present in *D. cornutus* and *D. trispinosus*. All PAT are preanal in *D. cobbi*, *D. demani*,

D. kreisi and *D. papuensis* females.

– Four species have more than 8 CAT: *D. cornutus* with 10–11 (σ), 10 (φ), *D. falcatus* with 12 CAT (σ , φ), *D. gertlachi* with 13 CAT (σ , φ) and *D. stekhoveni* with 14–15 (σ , φ).

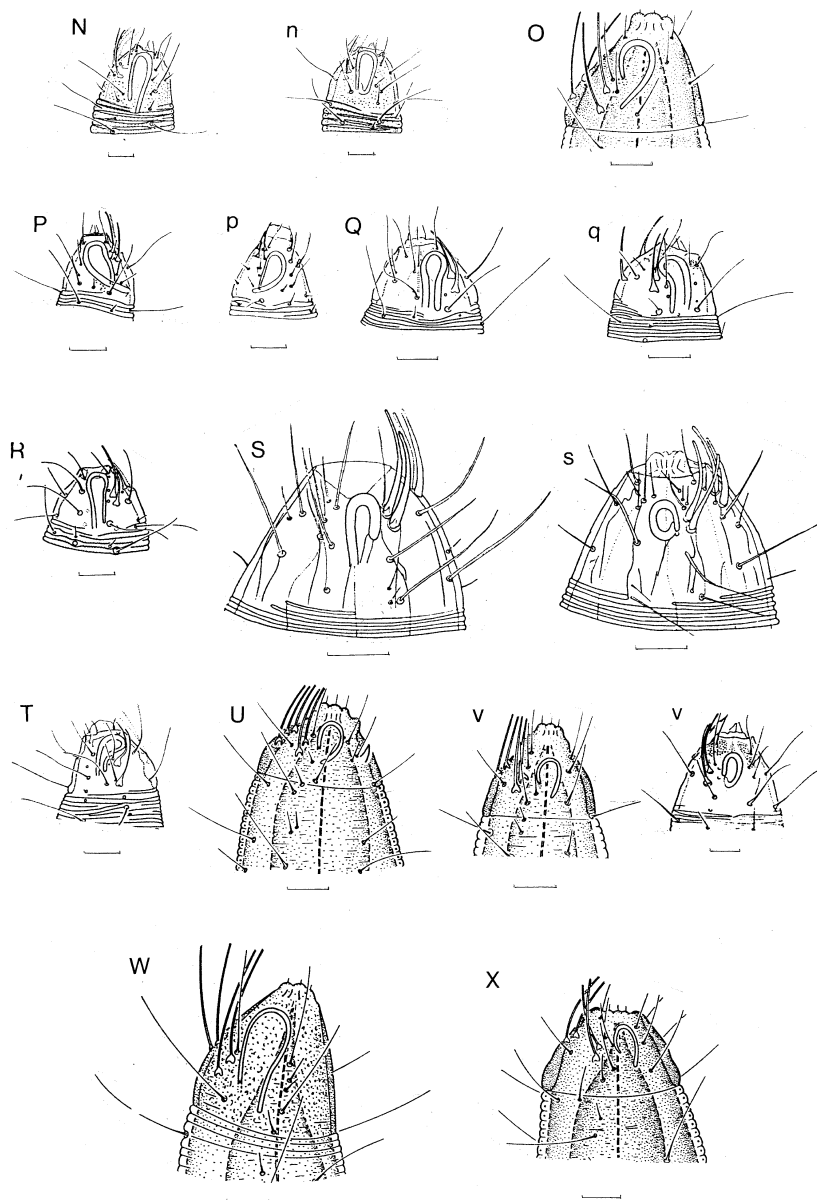


Figure 6b. (Q, q) *D. papuensis*, male, female; (R) *D. pusillus*, male; (S, s) *D. solidus*, male, female; (T) *D. spinosus*, male; (U) *D. stekhoveni*, male; (V, v) *D. timmi*, male, female; (W) *D. trispinosus*, male; (X) *D. wieseri*, male. Scale is 10 μ m. (O, U, V, v, W, X: after Allen & Noffsinger, 1978; N, n, P, p, Q, q, R, T: after Decraemer, 1988; S, s: after Gerlach, 1952; p, v: after Gourbault & Decraemer, 1992).

Genus Paradraconema Allen & Noffsinger, 1978
(Figures 1C, 1c; 7D; 8N)

Draconematinae. Swollen anterior body region 12–15% of total body length. Body annules may show an ornamentation of minute spines and subcuticular granulation. Cephalic acanthiform setae (Figure 7D), one or two pairs, small to pronounced, present on helmet. Twelve CAT located on helmet in two transverse rows.

Eyespots usually present in cephalic region. Amphids large, loop-shaped or spiral. Two pairs of paravulval setae may be present. One pair or a single precloacal copulatory thorn usually present. All PAT anterior to cloacal opening/anus.

Type species: Paradraconema floridense Allen & Noffsinger, 1978

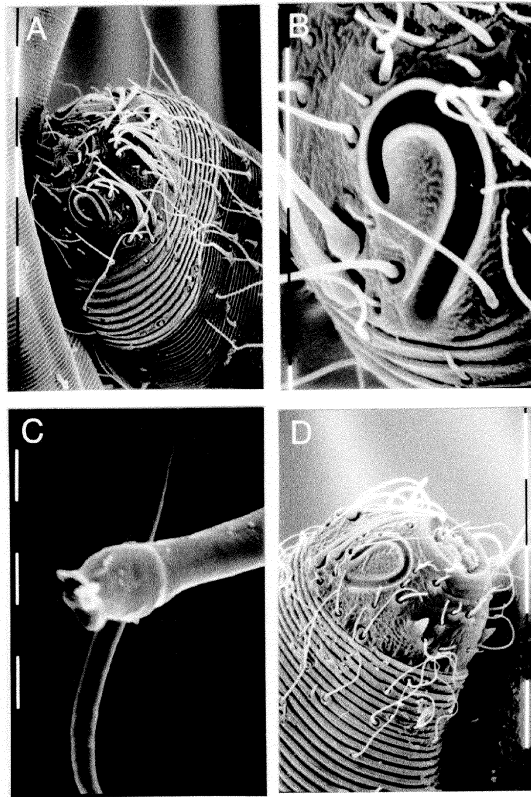


Figure 7. Scanning electron microscopic pictures: *Draconema haswelli*: (A), cuticular differentiation, female; (B) amphideal fovea in male; (C) detail of posterior ambulatory seta in male. *Paradraconema floridense*: (D), lateral view of helmet with amphidial fovea and cephalic acantiform seta. Scale 10 μm .

- *antarcticum* Allen & Noffsinger, 1978
- *californicum* Allen & Noffsinger, 1978
- *floridense* Allen & Noffsinger, 1978 [Decraemer, 1982] – (Figure 1C, c)
- *hopperi* Allen & Noffsinger, 1978
- *magentii* Decraemer, 1989
- *meridionale* (Kreis, 1937) Allen & Noffsinger, 1978
syn. *Draconema meridionale* Kreis, 1937
- *newelli* Allen & Noffsinger, 1978
- *singaporense* Allen & Noffsinger, 1978
- *spinosum* (Southern, 1914) Allen & Noffsinger, 1978
syn. *Chaetosoma spinosum* Southern, 1914;
Notochaetosoma spinosum (Southern, 1914) Cobb, 1929;
Drepanonema spinosum (Southern, 1914) Cobb, 1933;
Claparediella spinosum (Southern, 1914) Filipjev, 1934;
Draconema spinosum (Southern, 1914) Kreis, 1938

Subfamily *Prochaetosomatinae* Allen & Noffsinger, 1978

syn. *Cygnonematinae* Allen & Noffsinger, 1978;
Dracognominae Allen & Noffsinger, 1978; *Notochaetosomatinae* Allen & Noffsinger, 1978

Draconematidae. Pharynx largely cylindrical with terminal bulb well defined or weakly developed (e.g. *Dracogalerus*, *Notochaetosoma*); medium swelling of corpus present in *Dracognomus*. Swollen anterior body region usually marked; helmet present (except in *Dinetia*). CAT, with or without swollen base of insertion, with or without open tip, located on helmet or posterior to helmet. Buccal cavity small or moderately to well developed with one dorsal tooth, with or without two small subventral teeth; exceptionally narrow and unarmed (*Dinetia*, *Dracogalerus*, *Notochaetosoma*). Type genus *Prochaetosoma* Micoletzky, 1922 Several genera of this subfamily are monospecific. *Eudraconema* described in Bussau (1993) was considered a nomen nudum (for discussion see Decraemer & Gourbault, 1997).

Apenodraconema Allen & Noffsinger, 1978 (Figures 2B, 2b; 8E)

Prochaetosomatinae. Slightly swollen anterior body region 12–14% of total body length. Body annules with spiny ornamentation, cuticle thin. Eight CAT with swollen base of insertion and clearly open tip, arranged on two transverse rows within one head diameter posterior to helmet. Amphids open spiral in male, spiral in female. PAT short and straight, with bell-shaped tip; all anterior to cloacal opening/anus. Buccal cavity weakly developed with a small dorsal tooth. Pharynx about cylindrical, posteriorly slightly swollen, its lumen wall non-thickened. Tail spine-like with few annules.

Type species: *Apenodraconema chlidosis* Allen & Noffsinger, 1978

- *chlidosis* Allen & Noffsinger, 1978; [Gourbault & Decraemer, 1992]
- *spinicaudatum* (Gerlach, 1958) Allen & Noffsinger, 1978; [Decraemer, 1982]
syn. *Draconema spinicaudatum* Gerlach, 1958

Bathychaetosoma gen. nov. (Figures 5C, 5c; 8I)
syn. *Cephalochaetosoma* Kito, 1983 (*in partim*)

Prochaetosomatinae. Slightly swollen anterior body

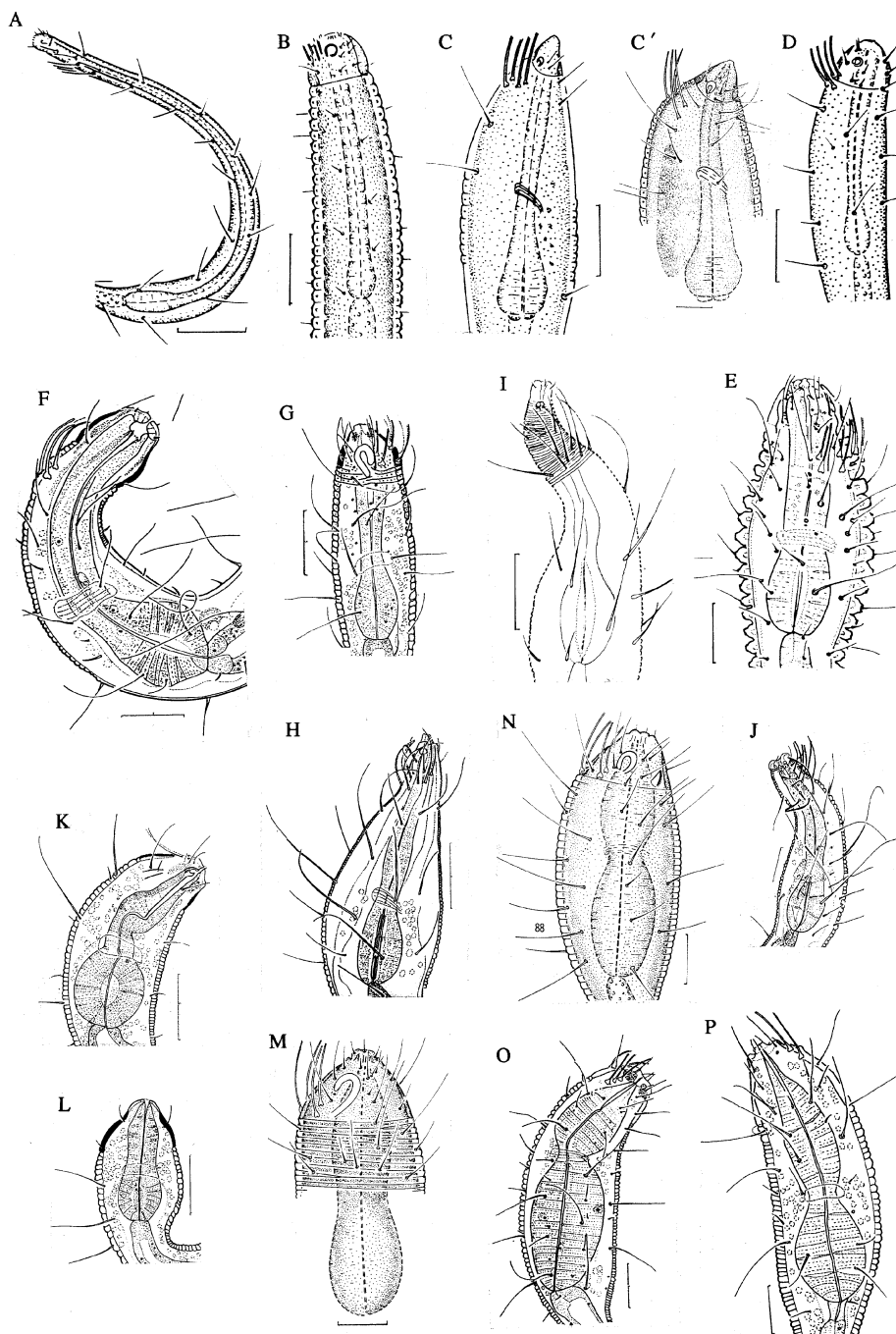


Figure 8. Different types of pharynx structure in the Draconematidae. – Pharynx more or less cylindrical with slight posterior swelling: (A) *Cygnonema steineri*, male; (B) *Dracogalerus bastiani*, female; (C, C') *Draconactis cutus*, female; (D) *Notochaetosoma tenax*, male; (E) *Apenodraconema chlidosis*, male. – Pharynx with endbulb well developed: (F) *Prochaetosoma martensi*, female; (G) *Tenuidraconema fieri*, male; (H) *Dinetia nycterobia*, male; (I) *Bathychaetosoma uchidai*, male; (J) *Cephalochaetosoma pacificum notium*, male. – Pharynx with endbulb well developed and mid-corpus swelling. (K) *Dracognomus marioni*, male; (L) *Dracognomus simplex*, male. – Pharynx dumbbell-shaped: (M) *Draconema haswelli*, male; (N) *Paradraconema meridionale*, male; (O) *Dracograllus cornutus*, male; (P) *Dracograllus minutus*, male. Scale = 20 μm exc. 80 μm in A; 10 μm in C', P and 40 μm in B, D). A-D, M-N: after Allen & Noffsinger, 1978; E: after Gourbault & Decraemer, 1992; F-G: after Decraemer, 1989; H, J: after Decraemer & Gourbault, 1997; I: after Kito, 1983; K-L: after Decraemer & Gourbault, 1986; O-P: after Decraemer, 1988).

region 23–24% of total body length. Annulated body cuticle thin, with minute spines. Cephalic region differentiated, cuticle smooth, not thickened. Numerous CAT (16–18) with base non-swollen and fine open tip, located posterior to the head region and extending to more than two head diameter along the cervical region. Amphids open spiral in male, spiral in female. Buccal cavity well developed, armed with a dorsal and two small subventral teeth. Pharynx with terminal bulb; lumen wall of bulb moderately swollen. PAT with bell-shaped end, all anterior to cloacal opening/anus. Tail cylindro-conoid, with numerous annules.

Type species: Bathychaetosoma uchidai (Kito, 1983) new.comb.

Relationships

The new genus *Bathychaetosoma* is erected because it appears to have an intermediate position within the subfamily i.e. between *Cephalochaetosoma* and *Dinetia* based on differences in the structure of the helmet i.e. without a thickened cuticle.

Cephalochaetosoma Kito, 1983 (Figures 5B, 5b; 8J)

Prochaetosomatinae. Slightly swollen anterior body region 16–19% of total body length. Cuticle thin, smooth or with minute spines. Helmet present. Numerous CAT (18–27) with non-swollen base and open tip, located posterior to the head region and extending to about two head diameter along the cervical region. Amphids open spiral in male, spiral in female. Buccal cavity well developed, armed with a dorsal and two small subventral teeth. Pharynx with terminal bulb; lumen wall of bulb moderately swollen. PAT with bell-shaped end; all anterior to cloacal opening/anus. Tail cylindro-conoid with numerous annules.

Type species: Cephalochaetosoma pacificum Kito, 1983

- *C. pacificum notium* Decraemer & Goubault, 1997
- *C. pacificum pacificum* Kito, 1983 [Decraemer & Goubault, 1997]

Cygnonema Allen & Noffsinger, 1978 (Figures 4A, 4a; 8A)

Prochaetosomatinae. Very slender body with slightly swollen anterior region 22% of total body length. Cuticle thin, smooth. Ten CAT with swollen insertion base and blister-shaped tip, located posterior to helmet and extending over more than two head diam-

eter along the cervical region. Amphids loop-shaped in male, derived loop-shaped (tubular outline of one loop branch) in female. Buccal cavity weakly developed with a clear dorsal tooth. Pharynx long cylindrical with terminal swelling with non-thickened lumen wall. PAT short, straight, with bell-shaped end; all anterior to cloacal opening/anus. Tail cylindro-conoid with numerous rings.

Type species: Cygnonema steineri Allen & Noffsinger, 1978

Genus Dinetia Decraemer & Goubault, 1997

(Figures 5D, 5d; 8H)

Prochaetosomatinae. Slightly swollen anterior body region 22–23% of total body length. Cuticle thin and smooth. Body annulation reaching the lipregion and including the spiral amphids (male, female), cuticle not thickened in head region; no helmet. CAT, 15–19, without expanded base, located in cervical region. Buccal cavity narrow, unarmed. Pharynx with terminal bulb provided with a moderately thickened lumen wall. PAT with bell-shaped end; all anterior to cloacal opening/anus. Tail cylindro-conoid with numerous annules.

Type species: Dinetia nycterobia Decraemer & Goubault, 1997

Dracogalerus Allen & Noffsinger, 1978 (Figures 3B, 3b; 8B)

Prochaetosomatinae. Anterior body region hardly swollen, 13% of total body length. Body cuticle thick and smooth. Helmet present. Eight to twelve CAT with base not swollen and open tip, located anteriorly on helmet. Amphids spiral in male, open spiral or spiral in female. Buccal cavity narrow, unarmed. Pharynx about cylindrical, lumen wall not swollen in terminal part. PAT with bell-shaped end; all anterior to cloacal opening/anus. Tail cylindro-conoid with 10 annules or less.

Type species: Dracogalerus afrikaanus Allen & Noffsinger, 1978

- *afrikaanus* Allen & Noffsinger, 1978
- *bastiani* Allen & Noffsinger, 1978
- *cryptocephalus* (Irwin-Smith, 1918) Allen & Noffsinger, 1978
- syn. *Notochaetosoma cryptocephalum* Irwin-Smith, 1918

Dracognomus Allen & Noffsinger, 1978 (Figures 2D, 2d; 8K-L)

Prochaetosomatinae. Slightly swollen anterior body region, 13–17% of total body length. Cuticle thin and smooth. Head asymmetric, ventral side shorter. Helmet present (except in *D. simplex* with CAT just posterior to helmet). Eight CAT, fine, without swollen base and with fine open tip, located on helmet (except in *D. simplex*). Amphids reduced, inverted U-shaped or tubular, located at level of head-base and first body rings. Buccal cavity weakly developed with a small dorsal tooth. Pharynx with terminal bulb and mid-corpus swelling; moderately thickened lumen wall in bulb. PAT without differentiated tip, often extending posteriorly beyond the cloacal opening/anus. PAT of two types: either all PAT modified or typical. Copulatory thorns or ventral expansions on tail may be present. Occurrence of paravulvar setae. Tail cylindro-conoid with numerous annules.

Type species: Dracognomus marioni Allen & Noffsinger, 1978

- *annae* Verschelde & Vincx, 1993
- *dermatoglyphus* Verschelde & Vincx, 1993;
- *marioni* Allen & Noffsinger, 1978; [Decraemer & Goubault, 1986]
- *notohalensis* Allen & Noffsinger, 1978
- *simplex* (Gerlach, 1954) Allen & Noffsinger, 1978; [Decraemer & Goubault, 1986]
- syn. *Draconema simplex* Gerlach, 1954
- *tinae* Jensen, 1981

Draconactus Allen & Noffsinger, 1978 (Figures 3C, 3c; 8C-C')

Prochaetosomatinae. Slightly swollen anterior body region 14% of total body length. Annulated body cuticle thick and smooth. Helmet present. Eight CAT short, straight, with slightly widened base and blister-shaped tip, located posterior to the head within one head diameter. Amphids spiral, laterodorsal at base of helmet. Buccal cavity weakly developed with minute dorsal tooth. Pharynx cylindrical, widened posteriorly, lumen wall not thickened. PAT with bell-shaped end; all anterior to cloacal opening/anus. Tail cylindro-conoid with numerous annules.

Type species. Draconactus cutus Allen & Noffsinger, 1978

- *cutus* Allen & Noffsinger, 1978
- *suillus* (Allgen, 1932) Allen & Noffsinger, 1978

(known from 1 stage juvenile IV only)

syn. *Chaetosoma suilla* Allgén, 1932; *Drepanonema suilla* (Allgén, 1932) Cobb, 1933; *Claparediella suilla* (Allgén, 1932) Filipjev, 1934; *Draconema suilla* (Allgén, 1932) Schuurmans Stekhoven, 1935

Remark

D. suillus was differentiated from *D. cutus* on a longer body. Allen & Noffsinger (1978) considered *D. suillus* a valid species because of stable taxonomic characters of fourth stage draconematid juveniles and distinctive characters given in the original description.

Notochaetosoma Irwin-Smith, 1918 (Figures 3A, 3a; 8D)

Prochaetosomatinae. About cylindrical with hardly widened anterior body region, 10% of total body length. Cuticle thin and smooth. Helmet present. Eight CAT, swollen at insertion base, tip fine, open, located at border of helmet and anterior body rings. Amphids open spiral in male, spiral or open spiral in female. Buccal cavity narrow, unarmed. Pharynx about cylindrical with slight posterior swelling, lumen wall in posterior part not thickened. PAT with bell-shaped end, all anterior to cloacal opening/anus. Tail cylindro-conoid with numerous annules.

Type species: Notochaetosoma tenax Irwin-Smith, 1918

- *killieri* Warwick, 1977
- *tenax* Irwin-Smith, 1918; [Allen & Noffsinger, 1978]

Prochaetosoma Micoletzky, 1922 (Figures 2A, 2a; 8F)

Prochaetosomatinae. Swollen anterior body region 14–20% of total body length. Cuticle thin, with spiny ornamentation. Helmet round. Amphids modified spiral, C-shape. CAT variable in number (4, 6, 8, 9 and 14), with enlarged base and located less than one diameter posterior to helmet. Buccal cavity moderately developed, armed with 3 teeth (dorsal tooth conspicuous). Endbulb of pharynx with a well thickened lumen wall. PAT with bell-shaped tip, all anterior to cloacal opening/anus. Paravulvar setae usually present. Tail cylindro-conoid with numerous annules.

Type species: Prochaetosoma primitivum (Steiner, 1916) Micoletzky, 1922; [Allen & Noffsinger, 1978].

- *arcticum* (Kreis, 1963) Allen & Noffsinger, 1978
- syn. *Draconema arcticum* Kreis, 1963
- *brighti* Jensen, 1986

- *campbelli* (Allgen, 1932) Allen & Noffsinger, 1978
syn. *Chaetosoma campbelli* Allgen, 1932; *Drepanonema campbelli* (Allgen, 1932) Cobb, 1933; *Claparediella campbelli* (Allgen, 1932) Filipjev, 1934; *Draconema campbelli* (Allgen, 1932) Schuurmans Stekhoven, 1935
- *cayense* Allen & Noffsinger, 1978
- *longicapitatum* (Allgen, 1932) Allen & Noffsinger, 1978
syn. *Chaetosoma longicapitatum* Allgen, 1932; *Drepanonema longicapitatum* (Allgen, 1932) Cobb, 1933; *Claparediella longicapitatum* (Allgen, 1932) Filipjev, 1934; *Draconema longicapitatum* (Allgen, 1932) Schuurmans Stekhoven, 1935
- *lugubre* (Gerlach, 1957) Allen & Noffsinger, 1978
syn. *Drepanonema lugubre* Gerlach, 1957
- *martensi* Decraemer, 1989
- *mediterranicum* Allen & Noffsinger, 1978
- *primitivum* (Steiner, 1916) Micoletzky, 1922
syn. *Chaetosoma primitivum* Steiner, 1916; *Draconema primitivum* (Steiner, 1916) Filipjev, 1918; *Drepanonema primitivum* (Steiner, 1916) Cobb, 1933; *Claparediella primitivum* (Steiner, 1916) Filipjev, 1934
- *vitielloi* Allen & Noffsinger, 1978 [Masalles, 1985]

Remark

- *P. primitivum* was described on a single fourth stage juvenile specimen. It was considered a valid species by distinctive characters (e.g. number of PAT) given in the original description by Allen & Noffsinger (1978). It can be differentiated from 5 other species of the genus with fourth stage juveniles known, but not from four other species with juveniles or fourth stage juveniles being unknown.
- The number of CAT is unknown for *P. lugubre*; 4 and 6 CAT are present in two species each; three species have 8 CAT and one species has resp. 9 CAT and 14 CAT. Only five species are known by both male and female.

Tenuidraconema Decraemer, 1989 (Figures 2C, 2c; 8G)

Prochaetosomatinae. Swollen anterior body region 8–10% of total body length. Body cuticle thin, with vacuolar ornamentation anteriorly and posteriorly, annules smooth in between with marked lateral alae. Twelve CAT with widened base and blister-shaped tip, located on the helmet. Amphids loop-shaped in male, spiral in female. Stoma narrow, unarmed. Pharynx with ter-

minal muscular bulb, lumen wall not thickened. PAT with developed bell-shaped end, all anterior to cloacal opening/anus. Tail spine-like with numerous annules.
Type species: Tenuidraconema fiersi Decraemer, 1989

Remark:

The relationship of *Tenuidraconema* is discussed upon the results of the phylogenetic analyses (see further).

Phylogenetic analysis of the family Draconematidae

For the 14 genera of the Draconematidae, up to 28 characters have been used in differential diagnoses. Half of these diagnostic features represent autapomorphies for individual genera. For example, presence of eyespots, presence of cephalic acantiform setae and pre-anal acantiform or corniform setae and position of sublateral adhesion tubes anterior to the cloacal opening/anus (*Paradraconema*), differentiated anterior body annules (*Draconema*), conical shape of rostrum (*Draconactus*), spine-like tail with few annules (*Apenodraconema*), absence of helmet (*Dinetia*), presence of a differentiated lateral field (*Tenuidraconema*). Autapomorphies, although taxonomically important, have no impact on the phylogenetic tree topologies based on cladistic analyses. Since current classification within the Draconematinae is largely phenetic, we were interested to find out to which extend the classification is phylogenetically supported.

Evaluation of diagnostic features (Table 1)

1. *General body shape*. In the Draconematidae, the body shape is mostly S-shaped, rarely epsilon, with a typical enlargement at the level of the pharynx (with ratio: maximum body width to minimum body width larger than 2), a habitus which is considered as an apomorphic feature. The almost cylindrical body is a plesiomorphic condition.

2. *Helmet*. Within the Draconematidae, a non-differentiated head region is considered plesiomorphic; the presence of a rounded well developed helmet with a more or less thickened and sclerotized annulated cuticle is apomorphic.

3–4. *Body cuticle and ornamentation*. Cuticular ornamentation shows few differentiations; the presence of wider annules in the anterior body region only (Figure 1a) or the presence of lateral alae are apomorphic features, based on ontogenetic comparison.

Table 1. Polarity of taxonomic characters at genus level within the Draconematidae

1. General body shape	0	cylindrical/almost cylindrical; $1 < \text{mbd}/(\text{mbd}) < 1.1$
	1	slightly enlarged at level of pharynx; $1.1 < \text{mbd}/(\text{mbd}) < 2$
	2	pronounced enlargement at level of pharynx; $\text{mbd}/(\text{mbd}) = > 2$
2. Helmet	0	absent (Figure 5d)
	1	present, cuticle more or less thickened, sclerotized (Figure 5 a,b)
3. Body cuticle	0	thin (Figure 1C)
	1	thick (Figure 3B, 3b)
4. Ornamentation of body cuticle	0	smooth
	1	presence of spines (Decraemer & Gourbault, 1997, Figure 7E)
	2	higher size of the first (7–14) body annules (Figure 7A)
	3	lateral alae present
5. CAT	0	modified (Figure 2d. Decraemer & Gourbault, 1997, Figure 6)
	1	typical (= with enlarged base) (Figure 1a)
6. Number of CAT	0	8 – 12 (rarely 4 or 6)
	1	> 13
7. Position of CAT	0	posterior to helmet, extending up to more than two head diameter along cervical region (Figure 4a)
	1	within one head diameter posterior to helmet (Figures 2a, b)
	2	on helmet (Figure 1)
8. PAT	0	modified (= without differentiated tip) (Figure 2D)
	1	typical (= with bell-shaped tip) (Figure 7C)
9. Amphidial fovea in male and female	0	spiral, loop-shaped (Figures 6, 6'; 7B, D)
	1	reduced inverted U shape (= tubular) (Figure 2d)
10. Buccal cavity	0	narrow, unarmed (Figure 3a)
	1	weakly developed with a small dorsal tooth (Figure 8E)
	2	moderately to well developed with a dorsal and two subventral teeth (Figure 8F)
11. Pharynx	0	more or less cylindrical, posteriorly slightly swollen (Figure 8B)
	1	pharynx largely cylindrical with endbulb well developed (Figure 8F)
	2	pharynx with mid-corpus swelling and endbulb well developed (Figure 8K, L)
	3	dumbbell-shaped, with swollen corpus and swollen endbulb (Figure 8 O)
12. Lumen wall of endbulb	0	non thickened (Figure 8B)
	1	moderately thickened (Figure 8L)
	2	strongly thickened (Figure 8F)
13. Number of annules on tail	0	> 10, numerous
	1	=/ < 10 (Figure 2B)

Table 2. Data matrix 1. Original data with splitting of the genera with intrageneric variables features (*)

Characters	1	2	3	4*	5	6*	7*	8	9	10	11	12	13
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Apenodraconema</i>	1	1	1	1	1	0	1	1	0	1	0	0	1
<i>Bathychaetosoma</i>	1	1	0	1	0	1	0	1	0	2	1	1	0
<i>Cephalochaetosoma 1</i>	1	1	0	0	0	1	0	1	0	2	1	1	0
<i>Cephalochaetosoma 2</i>	1	1	0	1	0	1	0	1	0	2	1	1	0
<i>Cygnonema</i>	1	1	0	0	1	0	0	1	0	1	0	0	0
<i>Dinetia</i>	1	0	0	0	0	1	0	1	0	0	1	1	0
<i>Dracogalerus</i>	0	1	1	0	0	0	2	1	0	0	0	0	1
<i>Dracognomus 1</i>	1	1	0	0	0	0	2	0	1	1	2	1	0
<i>Dracognomus 2</i>	1	1	0	0	0	0	1	0	1	1	2	1	0
Dracograllus 1	2	1	0	0	1	0	2	1	0	0	3	0	0
Dracograllus 2	2	1	0	0	1	1	2	1	0	0	3	0	0
<i>Draconactus</i>	1	1	1	0	1	0	1	1	0	1	0	0	0
<i>Draconema</i>	2	1	0	2	1	0	2	1	0	0	3	0	0
<i>Notochaetosoma</i>	0	1	0	0	1	0	1	1	0	0	0	0	0
<i>Paradraconema</i>	2	1	0	1	1	0	2	1	0	0	3	0	0
<i>Prochaetosoma 1</i>	1	1	0	1	1	0	1	1	0	2	1	2	0
<i>Prochaetosoma 2</i>	1	1	0	1	1	1	1	1	0	2	1	2	0
<i>Tenuidraconema</i>	2	1	0	3	1	0	2	1	0	0	1	0	0

5–7. *Cephalic adhesion tubes (CAT)*. The presence of CAT on the dorsal and dorsolateral side in the head region is unique in the phylum Nemata. Two different types have been observed: (1) with the insertion base swollen and a wide open tip (Figure 4a) and (2) with a non-differentiated base and fine tip (= modified type) (Figures 2d, 5b–d). The modified type of CAT resemble the setae in the Desmodoridae, and is considered plesiomorphic. The number of CAT is rather variable, but mostly 8/12; a large number of CAT is considered apomorphic upon ontogenetic comparison. Twelve CAT located on the posterior half of the helmet as in e.g. *Draconema* and *Paradraconema* is an apomorphic condition. The position of CAT posterior to the helmet for up to more than two head diameter, similar as cervical setae in Desmodoridae, is considered plesiomorphic.

8. *Posterior adhesion tubes (PAT)*. PAT are typical for the Draconematidae and Epsilonematidae, but both families differ by different insertion sites. In the Draconematidae, most PAT have the same length; rarely, long and short PAT are alternating on the same longitudinal rows. PAT with a bell-shaped enlarged tip containing a tongue-like triangular structure (Figure 7C) and in connection with well developed glands are considered apomorphic; PAT with a non-differentiated end (= modified PAT) tapered to a pointed tip as in somat-

ic setae are considered plesiomorphic. Two different types of PAT are present; they could represent different functions. Long and flexible PAT resemble common somatic setae (Figure 5A).

9. *Amphidial fovea in male and female*. Amphidial fovea, usually spiral and ventrally wound, as typical for Desmodoridae. The spiral shape is more common for females and juveniles than the loop-shape, with or without equally long branches, a derived spiral structure of males. The genus *Dracograllus* (Figures 6, 6') illustrates the large possible intrageneric variability of the spiral amphid shape (typical spiral to derived spiral), showing that further differentiation of 'spiral' amphids would not provide good diagnostic generic characters. The spiral or derived spiral amphidial fovea is a plesiomorphic condition. The 'aberrant', reduced inverted U or tubular shaped amphidial fovea is the apomorphic condition (Figure 2d).

10–12. *Buccal cavity and pharynx*. Buccal cavity narrow, unarmed and a cylindrical pharynx (Figure 7A) associated with a more cylindrical habitus as in the Desmodoridae, are considered plesiomorphic. The dumbbell-shaped pharynx with swollen corpus and endbulb (Figure 8O) typical for the three genera of the subfamily Draconematinae is apomorphic. A largely cylindrical pharynx with a well developed endbulb and a pharynx with a medium mid-corpus swelling (Fig-

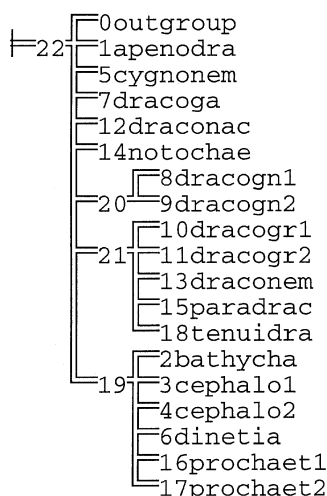


Figure 9. Strict consensus tree obtained from data set based on matrix 1 (Table 2), with characters non-additive.

ure 8K) and a more or less developed endbulb were considered as derived conditions. The interpretation of the different developing types may be slightly influenced by the condition of the specimen and the interpretation by the author e.g. Figures 8C, C' of *Draconactus acutus* with a more or less pronounced endbulb could be either characterized as a plesiomorphic condition or a more advanced one. Also the pharynx with mid-corpus swelling and endbulb as in *Dracognomus simplex* is close to the dubbell-shaped pharynx in *Draconema haswelli* (Figures 8 L and M).

13. *Tail*. The tail is mostly cylindro-conoid; it may possess an elongate terminal part with obvious spine-like shape (Figure 2B). A large number of annules on tail is frequent and was considered a plesiomorphic condition. The proportion of the non-annulated part of the tail to total tail length, usually ending with a spinneret, is a specific character, not a generic one.

Results of phylogenetic analysis

In an attempt to unravel the phylogenetic relationships among the genera of the Draconematidae (data matrix 1, Table 2), the presence of intrageneric variable characters 4 (=ornamentation of body cuticle), 6 and 7 (= resp. number and position of CAT) was dealt with by splitting up certain genera: *Cephalochaetosoma* (character 4), *Dracograllus* and *Prochaetosoma* (for feature 6) and *Dracognomus* (feature 7) respectively.

Figure 9 shows a strict consensus tree based on 5 MP trees (L=38, CI=57, RI=74) with all characters unordered and equally weighted. The genera which were splitted due to the presence of an intrageneric variable character, cluster together which means that they are well characterized. The data suggest two monophyletic groups and six genera of the *Prochaetosomatinae* with unresolved position. One monophyletic group is formed by the three genera of the *Draconematinae* (*Dracograllus*, *Draconema*, *Paradraconema*) + *Tenuidraconema*, which appears to belong to former subfamily. The second monophyletic group is formed by the deepsea genera (*Bathychaetosoma*, *Cephalochaetosoma*, *Dinetia*) and the genus *Prochaetosoma* of the *Prochaetosomatinae*. Within each monophyletic group the positions of the genera are unresolved.

Discussion

The current subfamilies *Draconematinae* and *Prochaetosomatinae* do not appear as monophyletic groups in the phylogenetic analyses. The genus *Tenuidraconema* appears to belong to the *Draconematinae* (instead of to the *Prochaetosomatinae*), a monophyletic assemblage characterized by feature 1 (= general body shape) and feature 11 (=pharynx). No resolution was proposed for the phylogenetic relationships of the four genera within this monophyletic group.

Taxonomically, the subfamily *Draconematinae* was originally differentiated from the subfamily *Prochaetosomatinae* by (1) the pharynx: dumbbell-shaped (= enlarged corpus + posterior bulb) vs cylindrical with a posterior swelling (exc. *Dracognomus* with a light medium swelling) and (2) buccal cavity very small and unarmed vs buccal cavity moderately developed and armed (rarely unarmed or narrow). *Tenuidraconema* has a narrow, unarmed buccal cavity but a largely cylindrical pharynx with a terminal bulb. The clustering of *Tenuidraconema* together with the three genera of the *Draconematinae* could indicate that the dumbbell-shaped pharynx was here secondary lost.

Based on the present phylogenetic analysis, we classify *Tenuidraconema* within the *Draconematinae*. The diagnosis of the subfamily *Draconematinae* is amended: 'pharynx dumbbell-shaped, exceptionally pharynx cylindrical with terminal bulb (*Tenuidraconema*)'.

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References

- (For references prior to 1973 see: Gerlach, S. & Riemann, F. (1973–1974). The Bremerhaven checklist of Aquatic nematodes. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven 4 (1,2), 734 pp.
- Allen, M. W. & E. M. Noffsinger, 1978. A revision of the marine nematodes of the superfamily Draconematoidea Filipjev, 1918 (Nematoda: Draconematina). *Univ. Calif. Publ. Zool.* 109, 133 pp.
- Bussau, C., 1993. *Taxonomische und ökologische Untersuchungen an Nematoden des Peru-Beckens*. Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel, 621 pp.
- Clasing, E., 1980. Post-embryonic development in species of Desmodoridae, Epsilonematidae and Draconematidae. *Zool. Anz.* 204: 337–344.
- Decraemer, W., 1982. Draconematidae and Epsilonematidae (Nematoda) from Laing Island Papua New Guinea, with one new genus and three new species. *Bull. Inst. r. Sci. nat. Belg. (Biologie)* 54: 1–22.
- Decraemer, W., 1988. *Dracograllus* (Nematoda: Draconematidae) from Papua New Guinea, with descriptions of new species. Leopold III Biological Station, Laing Island – Contribution no. 158. *Bull. Inst. r. Sci. nat. Belg. (Biologie)* 58: 5–27.
- Decraemer, W., 1989. Three new draconematid species from Papua New Guinea. *Bull. Inst. r. Sci. nat. Belg. (Biologie)* 59: 5–24.
- Decraemer, W. & N. Gourbault, 1986. Marine nematodes from Guadeloupe and other Caribbean Islands. II. Draconematidae. *Zool. Scr.* 15: 107–18.
- Decraemer, W. & N. Gourbault, 1997. Deep-sea nematodes (Nemata, Prochaetosomatinae): new taxa from hydrothermal vents and a polymetallic nodule formation of the Pacific (East Rise: North Fiji and Lau Bassins; Clarion-Clipperton fracture zone). *Zool. Scr.*
- Farris, J. S., 1989. Hennig 86: a PC-DOS program for phylogenetic analysis. *Cladistics* 5: 163.
- Gourbault, N. & W. Decraemer, 1992. Marine Nematodes from Polynesia. Epsilonematidae and Draconematidae. *Aust. J. mar. freshwat. Res.* 43: 663–681.
- Gourbault, N. & W. Decraemer, 1996. Marine nematodes of the family Epsilonematidae (Nemata): a synthesis with phylogenetic relationships. *Nematologica* 42: 133–158.
- Jensen, P., 1981. Description of the free-living marine nematode *Dracognomus tinae* n. sp. (Draconematoidea: Prochaetosomatidae). *Cah. Biol. Mar.* 22: 285–289.
- Jensen, P., 1986. The nematode fauna in the sulphine-rich seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. I. Chromadorida. *Zoologica Scripta* 14 (1985): 247–263.
- Kito, K., 1976. Studies on the free-living marine nematodes from Hokkaido. I. J. Fac. Sci. Hokkaido Univ., (serie VI, Zoology) 20: 568–578.
- Kito, K., 1979. Notes on the Postembryonic development of *Dracnema japonicum* Kito, 1976 (Nematoda: Draconematidae). *J. Fac. Sci. Hokkaido Univ., (Serie VI, Zoology)* 22: 88–98.
- Kito, K., 1983. Deep-sea nematodes off Mindanao Island, the Philippines. I. Draconematidae. *Anno t. zool. jap.* 56: 27–41.
- Lorenzen, S., 1974. *Glochinema* nov. gen. (Nematodes, Epsilonematidae) aus Süd-chile. *Mikrof. Meeresb.* 47: 1–22.
- Lorenzen, S., 1981. Entwurf eines phylogenetischen Systems der freilebenden Nematoden. *Veroff. Inst. Meeresforsch. Bremerh. (Suppl. 7)*, 472 pp.
- Lorenzen, S., 1994. The phylogenetic systematics of freelifving nematodes. – The Ray Society (translation) no 162: 383 pp.
- Masalles, D., 1985. Dos nuevos Draconematidae (Nematoda) para el Mediterraneo espanol: *Dracnema claparedii* (Metschnikoff, 1867), Filipjev, 1918, y *Prochaetosoma vitielloi* Allen & Noffsinger, 1978. *Invest. pesq.* 49: 155–164.
- Pastor de Ward, C. T., 1988. Nematodes marinos de la Ria Deseado (Desmodoroidea: Desmodoridae, Draconematidae), Santa Cruz, Argentina. VII. *Physis*, (Secc. A) 46: 61–72.
- Vershelde, D. & M. Vincx, 1993. Draconematidae (Nematoda, Desmodoroidea) from the Coast of Kenya, East Africa. *Bull. Inst. r. Sci. nat. Belg. (Biologie)* 63: 35–53.
- Vincx, M., 1986. Free-living marine nematodes from the Southern Bight of the North Sea. Ph.D. Dissertation, Ghent University.
- Warwick, R. M., 1977. Some free-living marine nematodes from the Isles of Scilly. *J. nat. Hist.* 11: 381–392.